Behavioural and anatomical correlates of sympathetic arousal and stress in male Central American Agoutis (*Dasyprocta punctata*)

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Abstract

Studied were distinctions and relationships between behavioural indicators of sympathetic arousal in twelve male Central American agoutis (six living in large groups and six in male-female pairs) in two social situations (pair-bonded and non pair-bonded). Indicators were scaled by correspondence analysis; scrapemark, scentmark (in pair living males), bury and scrape indicating high, scratch, nibble-of-body-sides, lick and tremble low sympathetic activity. Pair-bonded males displayed low and non pair-bonded males showed high amounts of behavioural elements indicating high sympathetic arousal. Morphologic-anatomical data were used for parallel analysis of long-term stress reactions. Pair-bonded males showed low and non pair-bonded males high relative portions of adrenal medulla at the central section area of adrenal glands. This can be regarded as adaptation to long lasting high sympathetic activity in the non pair-bonded males along with considerable stress reactions (enlarged hearts and diminished testes and anal glands). Thus the classification of males by their amounts of behavioural indicators of sympathetic arousal corresponds to their classification by physiological indicators of continuous sympathetic activity. The differentiating recording and analysis of appropriate behavioural elements provide a non invasive method for detecting arousal states and stress in individual animals, even in their "everyday life".

Introduction

In agoutis the social unit is a bonded pair in a defended area (Smythe 1978; Dubost 1988). In captivity the realization of social bonds is of central importance for the internal dynamics of the individual (Korz and Hendrichs 1989; Korz 1991). One important variable of these dynamics is arousal, meaning both the produced levels of general arousal and the locally produced states of specific arousal, both of which the animal is able to regulate depending on the quality of its social relationships (Korz and Hendrichs 1989). Social bonds (the integration of behavioural systems into a specific internal organization, Bowlby 1969) provide security (an internal state of an animal in correlation to the quality of internal organization) and hence prevent escalated arousal (Wickler 1976; Hendrichs 1988), which stresses the organism. Lack of social attachments can lead to considerable stress reactions (Henry and Stephens 1977).

For assessments of individual arousal in the agouti, frequencies of specific behavioural indicators have been used (Korz and Hendrichs 1989; Korz 1991). Findings in other rodent species indicate that these indicator elements are mainly correlated with sympathetic arousal. Application of adrenaline and noradrenaline produced higher frequencies of burying, scraping, scratching, and self grooming in rats (Maes 1979; Hawkins and Avery 1983; de Boer et al. 1990). In male agoutis variations of amounts of burying, scraping and

scentmarking displayed were correlated with variations in rhythmic and phasic components of body temperature (KORZ and HENDRICHS 1995). Males displaying decreased amounts of these elements when socially challenged, show decreased diurnal oscillations and increased mean body temperature. Hightened amounts were correlated with a more regular oscillation and decreased body temperature. In the generation of circadian oscillations of several physiological parameters in mammals the sympathicus is involved (REUSS 1993). The sympathoadrenomedullary system is mainly activated in animals which cope actively with social challenges while the pituitary adrenocortical system is more active in animals with inhibited behavioural activity (WEISS et al. 1970; HENRY and STEPHENS 1977; HOLST et al. 1983; SACHSER and LICK 1989).

The present study is based on data of twelve males, six living in larger groups and six in male-female pairs. The main aims were to elucidate relationships and distinctions between the different indicators of arousal, and to classify the males using the amounts of indicators they displayed. Anatomical and histological data were included for parallel analysis of long-term stress reactions.

Material and methods

Animals

Observed were three larger groups of agoutis, descendants of animals captured in Guatemala and bred at the Department of Ethology since 1974 (Tab. 1). For the first group (Group 1, consisting of 12 animals: the male M 1, four adult and two subadult females and five young animals) data were collected from June 1985 until February 1986 (120 hrs of observation), for the second group (Group 2, living since 1988 in the same enclosure and consisting of four males: M 23 (grown up in group 1), M 81, M 102, M 312, in that sequence of superiority; and six females) from November 1988 to May 1989 (56 hrs of observation). The third group (Group 3, consisting of one male: M 5, introduced into the group in July 1989, and five females) was observed from March to April 1991 (35 hrs of observation). Pair groups, living together for 6.5 months to 8.5 months, were observed from August 1990 until November 1992.

Housing conditions

The large groups were kept in roofed outdoor enclosures of 6.75 m to 9.00 m × 4.65 m with three adjoining wooden sleeping cabins each of 1.75 m × 1.10 m which were heated in winter. Pair groups were kept in adjacent roofed outdoor enclosures of 4.65 m × 2.25 m, each with an adjoining video-monitored

Table 1. Label, age, body weight and group membership of the observed males.

	Label	Age [years. months]	Body weight [g]	Group
GL	M 1	10.0	2 750	1
	M 5	10.0	3 300	3
	M 23	3.6	2 950	2
	M 102	2.0	2 780	2
	M 81	1.3	2 900	2
	M 312	0.6	2 500	2
PL	M 1 271	1.5	3 360	
	M 458	1.6	3 440	
	M 658	1.7	3 380	
	M 2 218	0.11	2 895	
	M 21 118	1.0		
	M 1 571	0.10		

GL: group living, PL: pair living

sleeping cabin (size as above). The cabins were illuminated by an electric bulb (75 watt) from one hour before observation to 15 min after the end of session. The enclosures contained branches and wooden or stony refuges where the animals were visible. The ground consisted of gravel covered with sand. The animals were exposed to natural light-dark-cycle. The ambient temperature varied from –10 °C to +30 °C for the large groups and from +6 °C to +26 °C for pair groups. The animals were fed on corn, rolled oats, fresh vegetables, fruits and leaves once a day (dry food and water ad libitum).

Behavioural data

The behaviour of animals was recorded by written entries in one-minute intervals as scan samples at 6–12 a. m. (large groups) and 17–21 p. m. (large and pair groups) when all animals were active. For each pair group a first quantitative observation phase (prephase) of five consecutive days in their home cages was followed by a testphase after the animals were set in a similar, but strange enclosure. After five days the pairs were set back into their home cages. For each phase ten hours of behavioural protocols were analyzed. The following behavioural elements were recorded:

Bite-attempt: A biting movement in the direction of another animal while sitting, standing or quickly approaching.

Bury: The animal takes a piece of food in its mouth, digs a hole into the ground with its forefeet, places the piece of food in the hole and covers it up, pressing the substrate with its forefeet.

Chase: The animal runs after another one for at least two meters.

Chin-raise: A male approaches a female with raised chin.

Drive: A male follows a female with raised chin for at least two meters.

Follow: A male follows a female in a distance of up to two meters.

Head-raise: Standing in front of or parallel to another animal at a distance of up to one meter the animal having raised its head stares at the other.

Head-thrust: The animal thrusts its raised head at another.

Joust: Standing opposite on their hind legs two animals drum on each other with their forelegs.

Lick: The animal raises a forefoot and licks it.

Nibble: The animal sits at the side of another nibbling the other's head region from ear to corner of the mouth.

Nibble-of bodysides: The animal nibbles at its flanks.

Nuzzle: The animal nuzzles the corner of another's mouth (mostly when the latter one has a piece of food in its mouth).

Scentmark: The animal drags its anal glands over the ground leaving a secretion.

Scrape: The animal scrapes the ground with its forefeet (can change into burying and vice versa).

Scrapemark: After scentmarking the animal scrapes the ground with its hindlegs.

Scratch: The animal scratches its flanks with its hind leg, turning its body.

Sniff: The animal sniffs at parts of another's body.

Tremble: Brief body-trembling with hair erected.

Urine-spray: A male approaches a female, raises its body and sprays a jet of urine in the direction of the female.

Anatomical data

All the males of Group 2 died within 30 days (May to June 1989): M 1 died in February 1986. The bodies, covered in plastic, were frozen at –20 °C within a few hours after death. In October 1989 the bodies were dissected after 18 hrs of thawing and organs were histologically and microbiologically examined. Body weights did not differ before freezing and after thawing. Hearts, kidneys, adrenal glands, testes and anal glands were weighed and fixed in 4% neutral formalin. For each body side, adrenal glands were divided in the largest sectional area parallel to the longitudinal axis. After imbedding in Paraplast[R], several sections were produced and stained with hematoxylin-eosin. The size of adrenal cortex and medulla for each body side was measured at a magnification 600× by planimetry, and the tissue area was determined in mm^2. In November/December 1991 four of the pair group living males were killed and dissected within an hour in the same manner as described above. The legal requirements for this procedure have been adhered to.

Statistics

The behavioural data were analyzed by correspondence analysis (CA), the morphological data by principal component analysis (PCA). These multivariate techniques are eigenvector methods of ordination developed to describe a set of intercorrelated variables in terms of a smaller number of factors and determines components of association between variables and populations. CA extracts components of an χ^2-"distance"-measure of association for frequency tables (Hill 1973), whereas PCA does this in a similar way for Euclidean distances and continued data. Eigenvalues separate the total information into r factors. For each factor a set of row and column coordinates is computed. Distances of dots from the origin indicate the distance from total profile of row and column vectors. Associated dots can be determined by neighbourhood along the axes (vertically or horizontally, not diagonally). CA has the advantage of simultaneous plotting of individual males and behavioural variables (amounts of behavioural elements). The analyses were carried out using the PCA and P4M paragraphes of the statistical computer program package BMDP (version 1990). Differences in group means of behavioural data were evaluated by use of the Mann-Whitney-U-test, of anatomical data by use of the Welch's t-test (each two-tailed). The criterion of significance was set at $p \leq 0.05$.

Results

Male-female relationships

Each group living male showed a preference for a specific female (defined as directing courtship behaviour more than twice as much towards a specific female than on average towards every female; Korz 1991).

The assessment of a social relationship, especially of a pair-bond, is more difficult in pair living than in group living males, because there is no possibility to separate the quality of relationship between pair mates towards other conspecifics. Exclusivity of behaviour between two animals not restricted to times of estrus indicates a pair-bond (Lamprecht 1973; Wickler 1976). Mutual and exclusive nibble was shown by the group living males M 1 and M 23 and specific females. Therefore, only these males (of the group living ones) are taken to be pair-bonded. The behavioural profiles of contact (nibble, nuzzle, follow, and sniff) and agonistic behaviour (chase, joust, head-thrust, head-raise, and bite-attempt) the pair living males displayed towards their females were compared to those of the group living males directed towards their preferred females. Behavioural amounts were analyzed separately for pair and group living males using the CA. The coordinates of all males for the first two axes were graphically displayed in figure 1. Spatial neighbourhood of pair living males to the pair-bonded group living males M 1 and M 23 indicates a similarity of behavioural profile. It is assumed that behavioural similarity indicates a similarity of relationships towards the females. Therefore, the pair living males M 2218 and M 658 are taken to be pair-bonded. A clear coordination of M 1571 and M 21118 to the division pair-bonded/non pair-bonded is not possible with the present data. All other males are regarded to be non pair-bonded.

Arousal-indicating behaviour

In a first step for evaluation of relations and differences of the arousal-indicating behavioural elements, the intercorrelations between variables were computed (Tab. 2). There are high correlation coefficients between bury and scrape on the one hand and scrape and the other variables on the other hand. Because of statistical dependency of data more significant correlation coefficients are to be expected than for the comprehension of the essential variance contributing variables are necessary. For reducing the variables to a single factor explaining most of the variability of data the profiles of these behavioural elements for each male were analyzed by CA, and the coordinates of the single elements were pro-
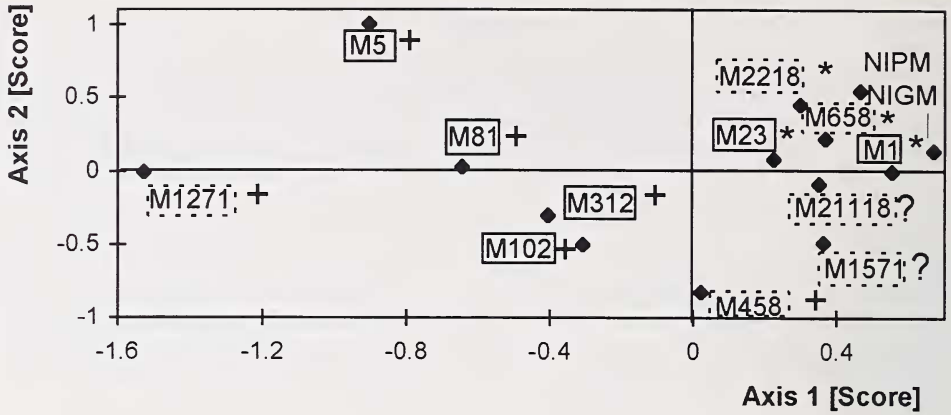
Fig. 1. Scores (χ^2-distances to the centroid) of group (N = 6, solid frames) and pair (N = 6, broken frames) living males for the correspondence analyses of amounts of contact and agonistic behavioural elements they displayed towards their respective females.
NIGM: Nibble occuring in groups, NIPM: Nibble occurring in pairs, *: pair-bonded males, +: non pair-bonded males, ?: no coordination possible.

jected on the first axis. The relative distances of elements from the origin of all elements and between coordinates of single elements along the axis are regarded as a scaling along a common dimension. Following the findings mentioned in the introduction, that occurrence and the frequencies of these behavioural elements are correlated to the sympathetic activity, the underlying dimension is seen as the sympathetic tone.

In figure 2 three situations are shown: an analysis for all males (group living males and pair living males in the prephase) without the elements scentmark and scrapemark and the analyses for pre- and testphase of the pair-living males considering these behavioural elements. Besides the fact that scrapemark was not displayed by group living males there is another reason for this differentiation: Scentmark is attached to territorial behaviour. It is shown by dominant males regularly while patrolling through their enclosure. Separating this kind of marking from spontaneously and arousal-indicating scentmarking is possible in the pair living males with comparable social status ("territory-holder with subordinated female"). Thus scentmark did not serve as arousal-indicating behaviour for group living males. The order of behavioural elements along the axis is following objective criteria, whereas the direction of axis depends on assumptions by the observer. The most simple assumption is that for a given sympathetic tone the probability of occurrence of a specific behavioural element presupposing a lower sympathetic tone is higher than

Table 2. Spearman rank-correlation coefficients for behavioural indicators of arousal.

	BU	SP	SC	NB	LI
SP	0.73*				
SC	0.55	0.74*			
NB	0.51	0.58*	0.85*		
LI	0.38	0.60*	0.77*	0.76*	
TR	0.44	0.64*	0.81*	0.78*	0.83*

BU: Bury, SP: Scrape, SC: Scratch, NB: Nibble-of-bodysides, LI: Lick, TR: Tremble. *: Critical values (df = 10, p < 0.05, two tailed).

for an element presupposing a higher sympathetic activity. The frequencies of behavioural elements and their corresponding axis scores should be negatively correlated. In the case of positive correlations the direction of axis was inversed. This procedure only affects the sign of the scores (Bond 1992). The three analyses are significantly indicating high probability of dependence between behavioural profiles along the specific axes (for all males χ^2: 1 328.5, df: 55, p < 0.001, two axes explaining 82.9% of the variability of data, axis 1: 62.4%, axis 2: 20.6%; for pair living males in the prephase χ^2: 1 374.5, df: 35, p < 0.001, two axes explaining 93.9% of the variability of data, axis 1: 60.8%, axis 2: 33.1%; and in the testphase χ^2: 1 810.1, df: 35, p < 0.001, two axes explaining 93.7% of the variability of data, axis 1: 50.8%, axis 2: 42.9%). The quasi-independence model allows the scaling of behavioural data of all males independently of their social situation. For more detailed information cf. Korz et al. (1995). For an assessment of the sympathetic tone the behavioural elements bury, scrape and nibble-of-bodysides closest correlated with the first axis (Tab. 3), and the first two ones distinctly separated from the other elements are of special importance. Nibble-of-bodysides indicates a low, bury and scrape a high sympathetic tone. For an animal displaying bury frequently the sympathetic tone is assessed to be higher than for an animal showing bury less frequently. In the prephase, under usual conditions, the element scrapemark points to a higher sympathetic tone than bury (hardly separated, not very evident); scentmark supplies no further information besides scrape. In addition, scentmark and scrapemark are not well represented on the first axis (Tab. 3). In the analysis of the testphase, under social conditions that stresses the animals, the marking behaviours are clearly separated from bury and scrape, indicating a very high and possibly escalated sympathetic activity. Along with the increasing importance of the marking behavioural elements they are now fit to the first axis (Tab. 3). The meaning of scrape and its correlation with the first axis decrease. High correlation coefficients indeed only imply how good the respective elements can substitute the combination of all elements. In order to get an appropriate interpretation of the axis the linear combination of all variables has to be taken into account (Harris 1985; James and McCulloch 1990). For pair living males displaying high amounts of scrapemark and bury a higher sympathetic tone is assessed than for males showing these elements less frequent, or, in the case of scrapemark, not at all. It was not an aim to construct a numerical scale, but to arrange the behavioural elements with respect to relative importance for an assessment of sympathetic activity.
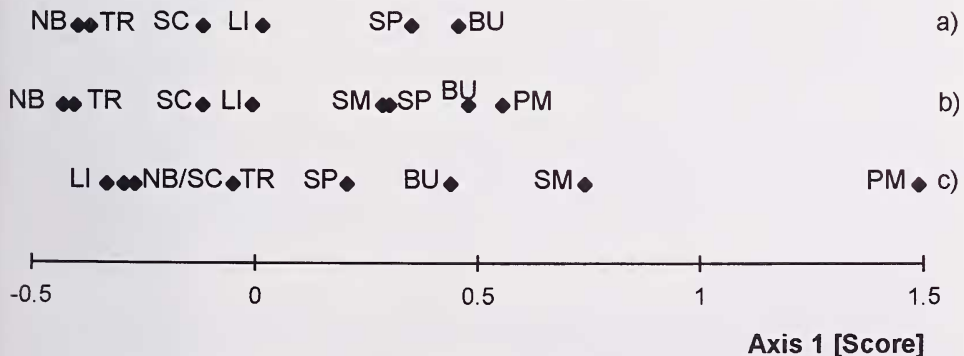
Fig. 2. Scaling of behavioural indicators of sympathetic arousal by correspondence analysis. a): analysis for all males (N = 12) group living males and pair living males in prephase, b): analysis for pair living males (N = 6) in prephase, c): analysis for pair living males (N = 6) in testphase (ten hours each). Given are the χ^2-distances to the centroid.
BU: Bury, SP: Scrape, SC: Scratch, NB: Nibble-of-bodysides, LI: Lick, TR: Tremble, SM: Scentmark, PM: Scrapemark.

Table 3. Correlation of profiles of behavioural indicators of sympathetic arousal and behavioural profiles of individual males with the first two axes (A1, A2) of correspondence analysis.

| | Group living males | | Pair living males | | | | all males | |
| | | | Prephase | | Testphase | | | |
	A1	A2	A1	A2	A1	A2	A1	A2
BU	0.56	0.04	0.76	−0.20	0.86	0.00	0.50	0.40
SP	−0.80	0.19	0.59	0.38	0.12	0.88	0.83	−0.05
SC	−0.01	0.15	−0.53	−0.01	−0.56	−0.07	−0.15	−0.10
NB	0.92	0.05	−0.97	−0.01	−0.57	−0.30	−0.85	0.10
LI	0.00	−0.91	0.00	0.54	−0.79	−0.04	0.01	−0.62
TR	−0.28	−0.61	−0.81	−0.10	−0.04	0.03	−0.37	−0.17
SM			0.16	−0.81	0.68	−0.32		
PM			0.05	−0.67	0.65	−0.34		
M 23	−0-06	−0.91						
M 81	−0-03	0.34						
M 102	0.85	0.02						
M 312	0.80	0.01						
M 1	0.00	−0.65						
M 5	−0.95	0.04						
M 1271			0.12	−0.86				
M 458			0.44	−0.16				
M 658			−0.96	0.00				
M 2218			0.55	0.04				
M 21 118			−0.03	0.90				
M 1 571			0.62	0.34				

Correlation: ratio between squared length of the projection on the axis from the origin and the squared distance from the origin in all dimensions (the signs result from those of coordinates). For abbreviations see Fig. 2.

In a second step the association of individual males to specific behavioural elements was analyzed. Figure 3 shows the results of the analyses for group (Fig. 3 a) and pair (Fig. 3 b) living males (group living males χ^2: 350.8, df: 25, p < 0.001, two axes explaining 89.6% of the variability of data, axis 1: 67.7%, axis 2: 21.9%; for pair living males see above). The classification of group living males is not explainable by the differences in age (Tab. 1) but by their different social situation (Fig. 1). The non pair-bonded males are associated with elements which point to a high sympathetic arousal like bury and scrape (group living males) as well as scrapemark, bury and scentmark (pair living males), whereas the pair-bonded males are associated with low sympathetic arousal indicating behavioural elements like lick, nibble-of-bodysides and tremble. M 2218 is arranged between the low sympathetic tone indicating element lick and the higher sympathetic tone indicating scrape (Fig. 3 b).

To summarize the analysis of behavioural indicators of sympathetic arousal gives the result that pair-bonded males, whether living in large groups or in pair groups, show on the average a lower level of sympathetic arousal than non pair-bonded males.

Comparing the frequencies of behaviour indicating high sympathetic arousal (bury, scrape and scentmark) between group and pair living males, there is an unexpected result (Fig. 4). Pair living males show significantly higher frequencies of these behaviours than group living males. One should assume that the life in large groups with high rates of agonistic encounters is more stressful than life in pair groups with a subordinated female.
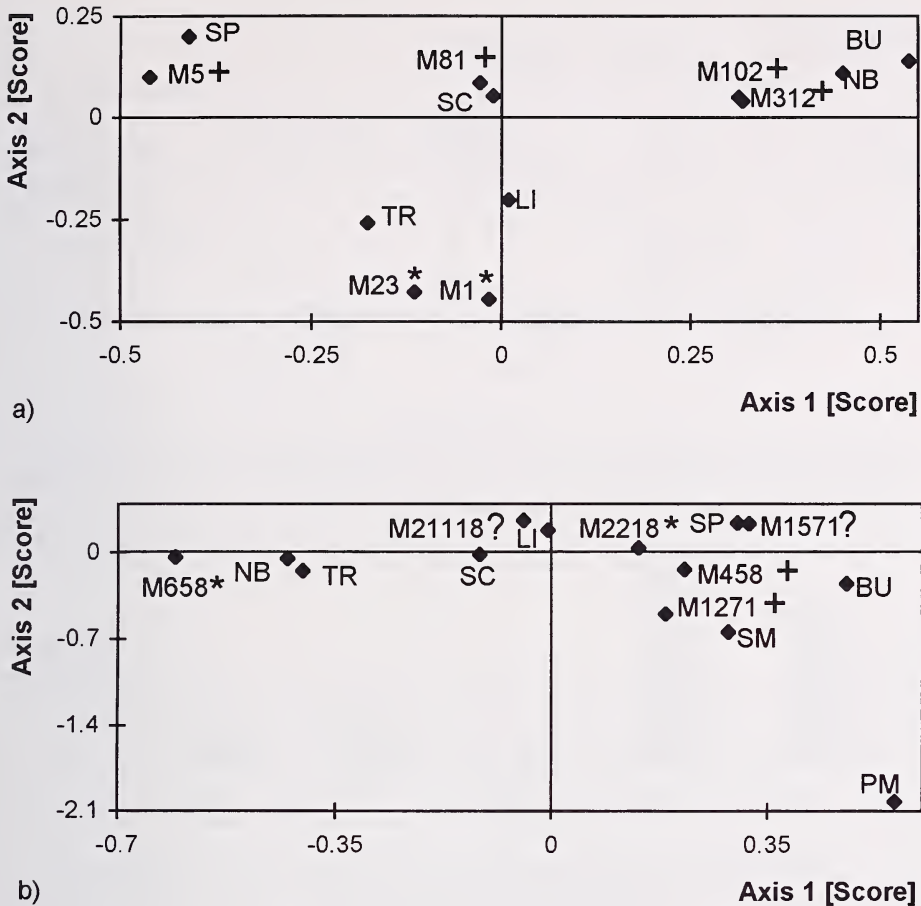
Fig. 3. Results of correspondence analyses of amounts of behavioural indicators of sympathetic arousal for group living (a) and for pair living (b) males. Labels for males are framed. Given are the χ^2-distances to the centroid.
*: pair-bonded males, +: non pair-bonded males, ?: no coordination possible. For abbreviations see Fig. 2.

This result points out that because of the very stressfull life in group living males not mainly the sympathicus adrenomedullary system but also the pituitary adrenocortical system is highly activated effecting the behavioural output. Additional data presented in the next paragraph contribute to this explanation.

Morphologic-anatomical indicators of long-term stress

Group living males showed significantly higher relative weights of adrenal glands (0.29 +/–0.10, Fig. 5) and lower body masses (2 776.0 +/– 175.0 g) than the pair living males (arithmetic average of relative weights of adrenal glands: 0.14 +/– 0.02, t = 3.08, p = 0.03, df = 4.5; average of body masses: 3 268.7 +/– 251.5 g, t = –3.33, p = 0.02, df = 5.2; Welchs' t-test). The absolute weights of adrenal glands are also significantly higher in group living (0.79 +/– 0.26 g) than in pair living (0.47 +/– 0.09 g, t = 2.53, p = 0.05, df = 5.2) males, while testes weights are higher in pair living (9.42 +/– 0.80 g) than in group living
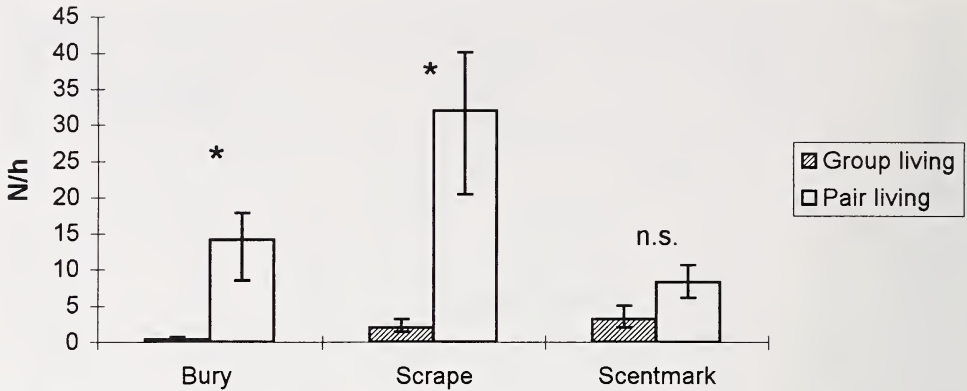
Fig. 4. Frequencies of bury, scrape and scentmark of group living (N = 6) and pair living (N = 6, prephase) males.
Median with interquartile range. N/h: average amount of behavioural element per hour. Statistics: Mann-Whitney-U-test, two tailed, *: indicates significant differences: U = 0, p < 0.01; n. s.: not significant.
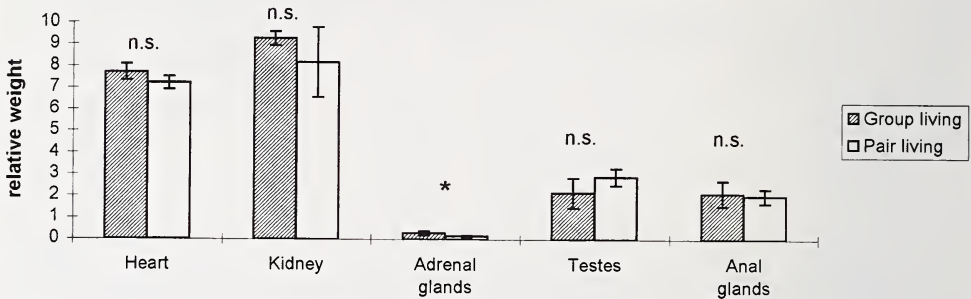

Fig. 5. Relative weights of organs of group (N = 5) and pair (N = 4) living males.
Arithmetic average and standard deviation. Statistics: Welchs' t-test, two tailed, *: p = 0.03; n. s.: not significant. Relative weight in $^0/_{00}$ of body weight.

(6.21 +/– 2.22 g, t = –2.99, p = 0.03, df = 5.2) males (given are the arithmetic average and standard deviation). The absolute weights of hearts, kidneys and anal glands did not differ significantly between group and pair living males.

For individual profiles of organic parameters the data were analyzed by principal component analysis (Fig. 6). Factors are orthogonally rotated by the Varimax-method. Two factors explain 65.3% of data variance (first factor: 36.4%, second factor 28.9%). The first factor accounts for the difference between males in respect of the relative portions of adrenal cortex and medulla at the central section area of adrenals, indicating that these parameters mainly correlate together, not with a third one. The second factor is highly loaded by weights of hearts (positively) and anal glands (negatively) showing that males with high heart weights exhibit small anal glands.

It depends on the condition of M 102 that heart weigths and relative portions of adrenal medulla did not highly load on the first factor with same sign. This is the only non pair-bonded male exhibiting a small portion of adrenal medulla at the central section area of adrenals. At the same time he is the most stressed male indicated by the fact that he shows the highest relative weight of adrenals (0.38) of all males and by additional findings of autopsy: several stomach ulcerations, an enlarged spleen and, along with the highest weight of heart of all males, a myocarditis. Militzer and Reinhard (1982) observed an
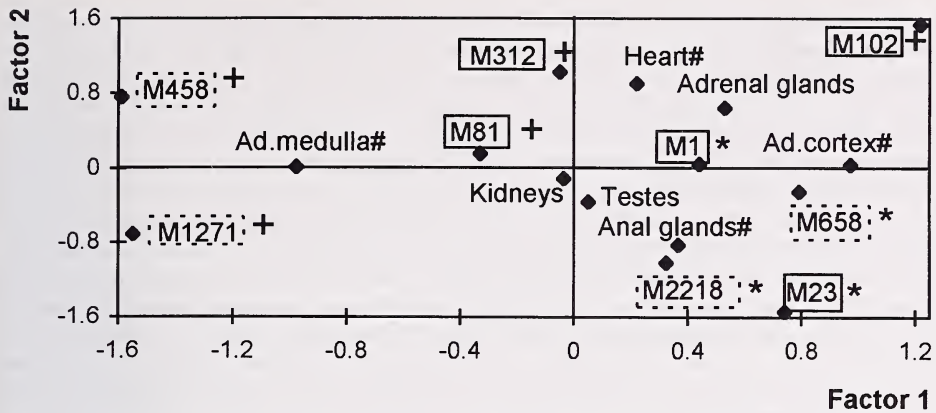
Fig. 6. Results of principal component analysis of relative weights of organs [$^0/_{00}$ of body weight], central section areas of adrenals [mm^2] and relative portions (%) of adrenal medulla and adrenal cortex at the central section area of adrenals of group (solid frames) and pair (broken frames) living males. Factor loadings of parameters and factor scores (χ^2-distances to the centroid) for individual males. Percentages are arcussinus-transformed. Ad. medulla: adrenal medulla, Ad. cortex: adrenal cortex, *: pair-bonded males, +: non pair-bonded males, #: indicates significant loadings, critical value for df = 7, p < 0.05: 0.666, two tailed.

increased adrenal cortex size along with a reduced adrenal medulla size in stressed rats. In the other males there were found: fat depots in abdominal cavity (M 81), spermatogonial giant cells in the testes of M 81 and M 102, pointing to degenerative processes probably effective in enhanced fertility (MILITZER and RASIM 1990). The separate analysis for the pair living males gives high positive loadings of heart weights and portions of adrenal medulla on the first factor. The arrangement of individual scores of the males shows that pair-bonded males associate with weights of testes and anal glands, suggesting a specific 'male status' and low stress. Proximity to the relative portion of adrenal cortex results from their corresponding low relative portion of adrenal medulla. M 1 and M 23 show the lowest absolute portions of adrenal medulla of all group living males. There were no symptoms of an increased activation of the pituitary adrenocortical system in pair-bonded males. The arrangement of non pair-bonded males points to effects of chronic stress, the males associated to relative portion of adrenal medulla at the central section area of adrenals (besides M 102) indicate continuously increased sympathetic activity with increased cardiovascular activity (M 458, M 81, M 312, M 102).

Discussion

The main question was aimed at the possible use of the relationships and distinctions of different behavioural indicators of arousal for a classification of the animals with regard to their sympathetic activation. The results were: a) behavioural elements indicated different levels of sympathetic arousal, b) frequencies of behavioural elements displayed by individual males differed according to their social situation (pair-bonded males displaying lower frequencies of high sympathetic arousal indicating behavioural elements than non pair-bonded males), c) classification of the males by behavioural amounts corresponded to their classification by anatomical and histological parameters (for the pair-bonded males indicating low and for the non pair-bonded males indicating high sympathoadrenomedullary activity).

The usual procedure is to combine different behavioural elements to more complex behavioural reactions, e. g. attack or withdrawal, for which a common motivation is assumed. The single elements may reflect different intensities of the underlying motivation, e. g. different states of escalated aggressiveness (Barlow and Ballin 1976; Bond 1992). By analyzing the behavioural reaction of an animal its motivational state can be characterized (Baerends 1976). Similarly the different behavioural elements, the single elements reflecting different levels of sympathetic arousal, can be combined to characterize the arousal state of an animal. Behavioural reactions can result from a mixture of different motivations. Display behaviour for example can be produced by sexual and by agonistic motivations, each accompanied by specific arousal processes. The elements were chosen for the following reasons: a) indicators should occur frequently enough to exclude chance influences, b) elements should not occur in immediate reactions towards conspecifics (to avoid direct social motivations), c) they should be comparable to elements found in other rodent species. The combination of elements is also significant because of the high intercorrelations.

A direct connection between sympathetic activity and the occurrence of this behaviour complex is not supposed, only that the complex hormonal and neural mechanisms leading to this behavioural output correlate with sympathetic arousal. Moreover, the assessment of arousal and stress using behavioural indicators is possible in a social field of regularly reacting animals, not in (pathologically) inactive animals.

The increased, but not disorganized or even stereotypic, specific motoric activity of non pair-bonded males can be seen as a coping response to elevated arousal. The possibility of displaying organized patterns of behaviour can serve as a behavioural release mechanism that can reduce damaging physiological effects (Conner et al. 1971). Such mechanisms are described e. g. for body temperature in the agouti (Korz and Hendrichs 1995), for the cardiovascular activity in rats (Fokkema and Koolhaas 1985). Levine and Wiener (1988) found lower plasma cortisol titers during high frequencies of vocalization in young squirrel monkeys (Saimiri sciureus), and Vanderwolf and Vanderwart (1970) and Elliott (1975) registered lower rates of heartbeat during increased frequencies of self-grooming in the rat. The pair living non pair-bonded males are in a position to cope actively with the social challenge of living and breeding with a female without a pair-bond. The group living males are even able to live closely with several conspecifics of both sexes. This capability is also found in group living females to such an extent that stress could be held low and reproduction remained possible (Korz 1991). Possibly the regulation of arousal challenges the non pair-bonded animals in a specific way. Compensating coping responses lead to behavioural and physiological hypertrophies and in the long-term to increased stress.

The higher masses of adrenal glands and the lower body weights in all group living males in relation to the pair living males point to higher stress of the first independent of dominance status and of whether they are pair-bonded or not. Possibly this can be explained by the particular challenges of group life with frequent social perceptions and activations. Among the group living males, however, the subordinated and non pair-bonded males are more stressed than the pair-bonded M 1 and M 23. The results in figure 6 and the additional findings mentioned point to an increased activity of the pituitary adrenocorticalsystem (M 102 and M 312), an inhibition of the pituitary gonadal system for all non pair-bonded males (leading to infertility in M 102 and M 81) and a considerable activation of the sympathoadrenomedullary system. The strong stress of the non pair-bonded, group living males can be seen as a result of subordination and the frequent agonistic behaviour of dominant animals together with the lack of a pair-bond. The comparable positions of non pair-bonded group and pair living males in figure 6 indicate that mainly the absence of a pair-bond leads to the described coping reactions. With regard to the finding that pair living males in spite of lower stress show significantly higher frequencies of high

sympathetic activity indicating behaviour than group living males, the following explanation is suggested: Along with an increased activity of the antagonistic vagus as an adaptation to chronic stress in group living males, the increased activation of pituitary adrenocortical system, indicated by the higher weights of adrenal glands, with high titers of cortisol possibly reduces the basal adrenomedullary activity. SZEMEREDI et al. (1988) found this effect during chronical glucocorticoid treatment in rats. Reflexive sympathoadrenomedullary activation was not affected. As mentioned above, high cortisol titers mainly are found in animals which hardly activate in behaviour, whereas a sympathoadrenomedullary activation is found in actively coping animals. HENRY and STEPHENS (1977) report an increased activation of both systems during chronic stress. An adjusting balance between these antagonistic activities may explain the lower frequencies of bury, scrape and scentmark in group living males. In pair living males the sympathetic tone accomplishes the production of higher frequencies of the behavioural elements. Thus the assessment of arousal and stress by behavioural indicators of an individual animal have to consider the living conditions. The physical and social environment are relevant for understanding physiological reactions during stress, as pointed out by HOLST (1977).

The differentiating recording and analysis of appropriate behavioural elements provide a non invasive method for detecting arousal states and stress in individual animals. Data on different physiological parameters (e. g. heart rate) may help to evaluate further which patterns of behaviour can reflect specific conditions of the animals.

Zusammenfassung

Verhaltens- und anatomische Korrelate zur Sympathikusaktivität und zu Belastungen bei männlichen Mittelamerikanischen Agutis (Dasyprocta punctata)

Es wurden Daten von sechs männlichen Mittelamerikanischen Agutis mit Weibchen in drei größeren Gruppen und sechs Männchen in ♂/♀-Paaren in zwei unterschiedlichen sozialen Situationen (paargebunden und nicht-paargebunden) analysiert. Geeignete Verhaltensindikatoren für die Aktivität des sympathischen Nervensystems (Futtervergraben, Scharren, Kratzen der Körperseiten, Knabbern der Körperseiten, Lecken der Vorderpfoten, Schütteln, Markieren und Scharrmarkieren) wurden mittels Korrespondenzanalyse hinsichtlich der Höhe des ihnen jeweils unterliegenden Sympathikotonus skaliert. Es zeigte sich, daß Futtervergraben und Scharren einen hohen und unter akut belastenden Bedingungen Markieren und Scharrmarkieren einen sehr hohen Sympathikotonus anzeigen. Paargebundene Männchen zeigten geringe und nicht-paargebundene Männchen hohe Mengen der einen hohen Sympathikotonus anzeigenden Verhaltenselemente. An fünf gruppenlebenden und vier paarlebenden Männchen konnten morphologisch-anatomische Daten für die Analyse langfristiger Belastungsreaktionen erhoben werden. Paargebundene Männchen zeigten niedrige und nicht-paargebundene hohe relative Anteile der Nebennierenmedulla an der zentralen Anschnittfläche der Nebennieren. Dieser Befund wird als Anpassung an langfristige hohe Sympathikusaktivität gesehen. Einhergehend mit dieser Aktivität, zeigten sich deutliche Stressreaktionen bei nicht-paargebundenen Männchen: erhöhte Herzmassen sowie verringerte Hoden- und Analdrüsenmassen. Die Klassifikation der Männchen anhand der Verhaltensparameter korreliert mit derjenigen anhand der physiologischen Parameter für langfristig erhöhte Sympathikusaktivität. Die differenzierte Erfassung und Analyse geeigneter Verhaltenselemente versprechen einen nicht-invasiven Zugang zur Erfassung von Erregtheitszuständen und Belastungen bei Tieren auch unter „Alltagsbedingungen".

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